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INHERITANCE OF SMOOTH AWN AND DISEASE REACTION IN BARLEY CROSSES

Walter Herald Johnston
Department of Field Crops.

University of Alberta,
Edmonton, Alberta.
April, 1933.

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FACULTY OF AGRICULTURE.

The undersigned hereby certify that they have read and recommend to the Committee on Graduate Studies for acceptance a thesis on "Inheritance of smooth awn and disease reaction in barley crosses," submitted by Walter Harold Johnston, B.A., B.Sc., in partial fulfilment of the requirements for the degree of Master of Science.

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A THESIS

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INHERITANCE OF SMOOTH AWN AND DISEASE REACTION IN BARLEY CROSSES.

W.H. Johnston

INTRODUCTION

The breeding of smooth awned barleys has received considerable attention in the last few years. The advantages possessed by this type of barley have been pointed out by Harlan (13) and need no further discussion. It is important that such a desirable character as smooth awn be associated with an equally desirable one, that of disease resistance. With the exception of the investigations of Hayes et.al. (17), and Griffee (12), practically no work regarding the breeding of smooth awned barleys for resistance to disease has been reported. This study was undertaken with the two-fold purpose of studying the relationships existing between smooth awn and reactions to the pathogenes Ustilago hordei (Pers.) K.& S., Ustilago nuda (Jens.) K.& S., and Helminthosporium gramineum Rabh. and to determine if possible the mode of inheritance of these characters. Genetic data were also compiled on earliness and height of plant and length of rachilla hairs.

The pathogenes referred to above were selected for this investigation because they are the causal agents of three of the more destructive diseases of barley occurring in Western Canada. Reports on the distribution and economic importance of these diseases in Alberta are given in the reports on "Prevalence of Plant Diseases in the Dominion of Canada," for the years 1927-31 (5,6,24).

In Alberta for the five year period covered smut is designated in all years as being "common and destructive, causing important losses". The report of 1931 (5), which is fairly typical, shows 50 percent of the fields examined to be infected, a few running as high as 70 percent infection.

Loose smut of barley is reported as being of widespread distribution but the loss being much less than that caused by covered smut. It is also a significant fact that investigators have noted that smooth awned varieties are generally susceptible to the loose smut disease.

The stripe disease is reported as being less important than either of the smut diseases. However, approximately 25 percent of the fields examined in Alberta in 1930 showed infected plants, with one field exhibiting 20-30 percent infection. Work conducted at the University of Alberta shows that a number of promising new varieties are susceptible to this disease. The practice of late seeding of barley probably accounts for the small percentages of infection noted in the surveys.

Mention has already been made regarding the dearth of literature concerning the breeding of smooth awned barleys for disease resistance. In fact, it may be said that as compared to wheat and oats, little work along disease resistance lines has been reported in barley. There are a number of reasons for this.

In the first place, the relatively lower economic value of the barley crop has not stimulated the same interest in the development of disease-resistant varieties as has occurred in wheat and oats. Furthermore, the early development of control measures did much to discourage any breeding investigations. Probably the most important factor handicapping the breeding of resistant varieties is the lack of a satisfactory inoculation technique for obtaining infection. Many difficulties are encountered if the seeds are dehulled. Dehulling by hand is impractible in large populations whereas the use of chemicals is still in the experimental stage and offers many difficulties. Floral inoculation is a very laborious process even when undertaken in the most favourable of conditions, as in the greenhouse. When carried out in the field, environmental factors render the results very uncertain. The weak straw of the barley plant aggravates the problem if the heads are to be bagged.

The presence of physiologic forms and a lack, in a great many instances, of adequate knowledge regarding the influence of environmental factors on infection, serve as further barriers to the obtaining of high percentages of smut in susceptible varieties.

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PARENTAL MATERIAL.

The barley varieties used in the investigation under consideration were two smooth awned types, Glabron and Velvet and a rough awned type, Trebi. Reciprocal crosses were made between Trebi and each of the smooth awned varieties.

Trebi is a six-rowed rough awned variety resulting from a pure line selection made in 1907 in the cooperative breeding experiments conducted by the United States Department of Agriculture and the Minnesota Agricultural Experimental Station, at St. Paul (15). This barley has bluish-grey kernels possessing short haired rachillas. It is weak strawed but yields exceptionally well. It is very susceptible to H. sativum; moderately susceptible to U. hordei; and resistant to U. nuda and H. gramineum.

Glabron and Velvet are six-rowed smooth awned varieties developed at the Minnesota Agricultural Experiment Station (18). Glabron was developed from a back-cross between Smooth Awn (a selection from a cross between Lion and Manchuria) and Manchuria, whereas Velvet resulted from a cross between Smooth Awn and Luth.

Glabron yields well and possesses a stiff straw. It is moderately susceptible to H. gramineum, susceptible to U. nuda and resistant to U. hordei and H. sativum. The kernels of this barley have the long-haired rachillas as compared to short-haired type possessed by Trebi.

Velvet is not quite so desirable from an agronomic point of view as Glabron. It is not only lower in yield but possesses a decidedly weaker straw. It is very susceptible to H. gramineum and U. nuda, but shows resistance to H. sativum and U. hordei.

GENERAL METHODS.

The reciprocal crosses of Velvet and Trebi were studied in the F_1 and F_2 only, whereas those of Glabron and Trebi were carried into the F_3. All generations were grown on the experimental plots of the University of Alberta. The F_2 and F_3 with the parental varieties were seeded in ten-foot rows, one foot apart. Approximately fifty seeds were sown per ten-foot row in the F_3.

Barbing of awns was studied in the F_1 and F_2 of crosses involving Velvet and Trebi, and in the F_1, F_2 and F_3 of the reciprocal crosses of Glabron and Trebi. All other characters reported in this paper were studied in the F_3 of crosses involving Glabron and Trebi, with the exception of length of rachilla hairs which was investigated in the F_2 of this cross.

The seeds of all F_2 plants with the exception of some 500 plants inoculated with a spore suspension of H. gramineum, were divided, when the number of seeds permitted, into three lots of approximately 50 seeds each.

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The seeds of all F_2 plants with the exception of some 500 plants inoculated with a smut susceptible to [illegible] [illegible], were divided, when the number of seeds permitted, [illegible] ts of approximately 30 seeds each.

These were sown in genetic, covered smut and loose smut nurseries, respectively. In the event of insufficient seed, the preference was given first to the genetic nursery and then to the covered smut nursery.

The seed of the F_2 plants, from which two heads had been inoculated with a spore suspension of H. gramineum, were seeded in both genetic and stripe nurseries.

INHERITANCE OF CHARACTERS.

Barbing of Awns

Literature review.

The first crosses between rough and smooth awned barleys to be recorded in the literature were made by Harlan in 1912 (13). He concluded from a study of these that the rough awned condition was dominant and a single factor was involved.

Extensive studies on the smooth awn condition in barley were made by Vavilov (39). He was able to obtain smooth awned types from the F_2 and F_3 of a cross between two rough awned varieties. Studies of numerous crosses between parents of varying degrees of smoothness resulted in complicated ratios. He concluded from his investigations that "five to six factors were necessary to explain the

form, character, density and arrangement of the teeth on the awn on the races studied".

Hayes et.al.(17) working at the Minnesota Experimental Station with the varieties Lion (smooth awned) and Manchuria (rough awned) report that all F_1 plants had rough awns, while the F_2 generation segregated in an approximate ratio of 3 rough awned plants to one smooth. To improve upon the method of determining the degree of smoothness an index system was devised. This was accomplished by dividing the total length of the awn by the portion barbed. The larger the index the smoother was the awn. All smooth awned F_2 plants bred true in the F_3 generation for the smooth awn condition. However, it was noticed that some bred true for only low indices, some only for high indices, whereas others produced plants of both low and high indices. A number of the F_3 lines classed as rough awned in the F_2 bred true , whereas others broke up into rough and smooth awned types reflecting the F_2 generation. The authors believe that in addition to one main factor difference between rough and smooth awn, modifying factors brought in by the rough awned parent are required to explain the different degrees of smoothness.

Griffee (12) was able to divide the F_2 of a cross Lion x Svansfale into three phenotypes based on an arbitrary index. The types, rough, intermediate-smooth and smooth were obtained in a 12:3:1 ratio, thus indicating a 2-factor difference. The results were explained on the bases of epistasis.

The factor R when present produces rough awns; the other factor S is hypostatic to R and in the absence of R produces intermediate-smooth condition. The double recessive rrss expresses the smooth awn type. Griffee also ~~experienced~~ noticed much variation in the degree of smoothness amongst smooth awned lines and for this reason supports the view of Hayes et.al., (17) that certain minor factors are operative.

Sigfusson (31) obtained results somewhat similar to those of Griffee. He classified the F_2 into four phenotypes as follows: (a) rough, (b) intermediate-rough, (c) intermediate-smooth and (d) smooth. The first two classes were totally barbed but the barbs of the second group were decidedly less scabrous than those of the first. The third group was smooth at the base only, whereas the fourth was smooth to a few centimetres of the tip. The distribution in the F_2 gave a very close fit to a 9:3:3:1. Sigfusson explained his results on a 2-factor basis as follows:

> "the factor R either single or in duplicate and in the absence of S produces the intermediate-rough condition and similarly the factor S in the absence of R produces the intermediate-smooth condition. The factor R is the main factor and produces a greater effect than S but both are necessary either singly or in duplicate to produce the fully rough class. The smooth class is the double recessive and has the genetic constitution rrss."

David (7) arrived at quite different conclusions ~~than~~ from any of his predecessors. His contribution to the question is of special interest since he worked with similar crosses to those reported in this paper, viz., Glabron x Trebi and Velvet x Trebi. The F_2 segregated into what appeared to be a normal 3:1. However, the F_3 behavior could not be explained on the basis of a 3:1 hypothesis for about 2/3 of the smooth awned F_2 plants gave rise to F_3 progeny segregating in the ratio of 3 smooth awned to 1 rough awned. As this suggested the presence of an inhibitor, David compared the F_2 data with the theoretical 13:3 ratio. The fit was found to be good. He assumed there was present a dominant factor A for smooth awn and a dominant factor I inhibiting smooth awn. The smooth awned parent had the constitution AAii, the rough awned parent, aaII.

Robertson, Deming and Koonce (30) as a result of F_2 study of a Coast x Lion cross confirmed the findings of Griffee (12) in that the segregation of the F_2 approached a 12:3:1. The index method of determining smoothness was utilized (17).

Recently Wexelson (42) found a single factor difference between rough and smooth awns. The smooth awned segregates are reported as being as smooth as the smooth awned parent.

[illegible]

[illegible]

[illegible]

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Recently Davidson (43) found a single factor difference between rough and smooth awns. The smooth awned [illegible]gates are regarded as being as smooth as the smooth [illegible] parent.

Methods and experimental results.

The degree of barbing of the awns was determined by simply passing the awns between the fingers, ~~aided~~ This ~~when necessary~~ was supplemented by the use of a hand lens. This simple and rapid method was adopted rather than the more complex index system, because of the large F_2 population to be studied and because it was thought that an arbitrary index might be concealing the true phenotypic classes.

An examination of a large number of plants of the smooth awned parent showed a considerable variation in the degree of barbing of the awns. This varied from a few barbs at the extreme tips of the awns to barbs extending one-quarter of the length of the awns.

The F_1 of all the crosses studied were rough awned. It was comparatively simple to separate the F_2 plants into two main groups. Those with completely rough awns and those with awns exhibiting some degree of smoothness. Greater difficulty was experienced in establishing classes within these two groups. After considerable study it was decided that the F_2 material fell into the following five classes:

1. Rough awned
2. Intermediate-rough awned
3. Smooth base
4. Intermediate-smooth awned
5. Smooth awned.

[illegible]

[illegible]

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2. Intermediate-rough awned
3. Smooth base
4. Intermediate-smooth awned
5. [illegible]

The first two classes have fully barbed awns; but the barbs of the second class are much less scabrous than those of the first. The awns of class 3 have barbs extending along 50-75 percent of their length, whereas, in class 4 the barbs seldom extend over 50 percent of the length of the awn and are not as scabrous. Class 5 reflects the smooth awn parental type. An average awn of each of the five classes is illustrated diagrammatically in Figure I. Considerable variation was observed within these classes and for this reason it was thought that environmental factors might be responsible for the intermediate-rough and smooth base classes. Accordingly, the segregation of F_2 plants for barbing of awn in the crosses studied have been based upon three phenotypes; rough, intermediate-smooth and smooth; the two rough classes and the two intermediate-smooth classes having been grouped.

This grouping suggested a 12:3:1 ratio of rough : intermediate-smooth : smooth awned plants. The actual segregations as compared to the theoretical 12:3:1 are given in Tables I and II. The fit of the actual to the theoretical in the crosses involving Trebi and Glabron, (Table I) is fairly good in some cases, but owing to the tendency to place a number of intermediate-smooth plants in the smooth awned class, the total population shows a poor fit to the theoretical.

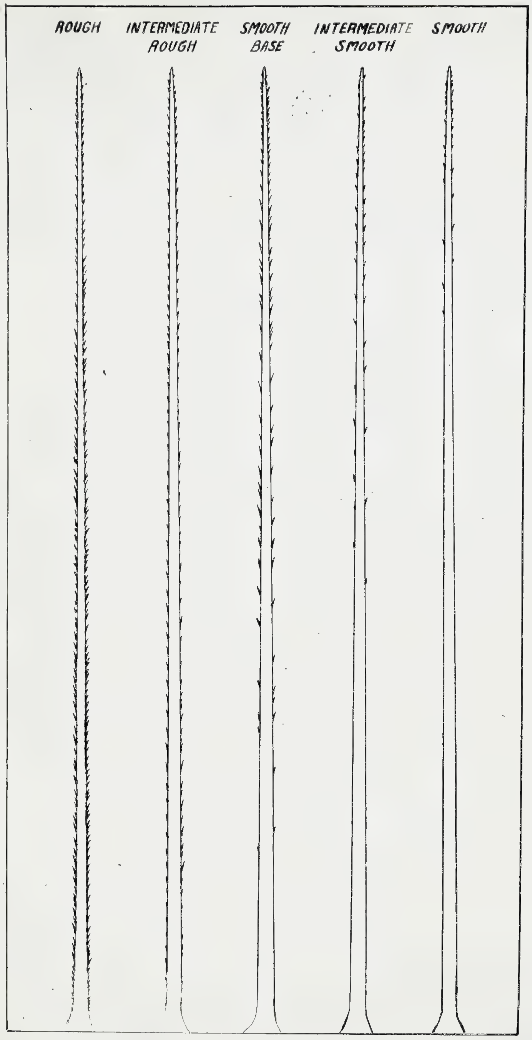

FIGURE I.

Diagrammatic length-wise section of average awn of each of five awn classes: Rough, intermediate-rough, smooth base, intermediate-smooth and smooth; used in classification of F_2 of reciprocal crosses Glabron and Trebi and Velvet and Trebi.

TABLE I.

Numbers of rough, intermediate-smooth and smooth awned plants in the F_2 generation of reciprocal crosses between Glabron and Trebi, as compared to the theoretical 12:3:1 ratio.

Cross	number.	Actual Rough	Actual Inter-mediate smooth	Actual Smooth	Theoretical Rough	Theoretical Inter-mediate smooth	Theoretical Smooth	X^2	P
Glabron x Trebi	6	111	21	7	104.28	26.07	8.69	1.75	0.43
	11	133	21	18	129.00	32.25	10.75	9.64	0.01
	12	170	32	16	163.50	40.88	13.63	2.60	0.28
	13	121	29	18	126.00	31.50	10.50	5.71	0.06
Trebi x Glabron	19	79	24	13	87.00	21.75	7.25	5.64	0.06
	20	158	33	14	153.75	38.44	12.81	1.00	0.61
	21	95	20	5	90.00	22.50	7.50	0.84	>0.61
	23	83	13	8	78.00	19.50	6.50	2.83	0.25
	45	136	22	10	126.00	31.50	10.50	3.68	0.16
Total		1086	215	109	1057.56	264.39	88.13	14.93	0.001

The reciprocal crosses of Trebi and Velvet together with their total show, on the other hand, good fits to the theoretical (Table II). This may be explained by the fact that as this cross was studied last, a greater familiarity with the different phenotypes was experienced.

TABLE II.

Numbers of rough, intermediate-smooth and smooth awned plants in F_2 generation of reciprocal crosses between Velvet and Trebi, as compared to the theoretical 12:3:1 ratio.

Cross	Number.	Actual			Theoretical			X^2	P
		Rough	Intermed.-Smooth	Smooth	Rough	Intermed.-Smooth	Smooth		
Trebi x Velvet	116	59	15	8	61.50	15.38	5.13	1.72	0.44
	123	160	30	12	151.50	37.88	12.63	2.15	0.35
	124	155	37	16	156.00	39.00	13.00	less than 1	>0.61
	133	186	50	19	191.38	47.82	15.94	1.73	0.43
Velvet x Trebi	137	183	45	16	183.00	45.75	15.25	less than 1	>0.61
	146	123	22	6	113.16	28.29	9.44	3.51	0.18
	148	188	41	14	182.28	45.57	15.19	less than 1	>0.61
	151	114	23	8	108.72	27.18	9.06	1.02	0.60
Total		1168	263	99	1147.56	286.89	95.63	2.47	0.30

The F_2 data just presented would seem to indicate a two factor difference for barbing of awn. It can be explained on the basis of epistasis; R is the main factor for barbing of awn; S is hypostatic to R and in the absence of R produces the intermediate-smooth condition, while the double recessive produces the smooth awn type. On the basis of

this hypothesis the F_2 plants, when tested in the F_3, should breed as follows:

Rough-awned plants;

4 Breeding true for rough

4 Segregating in the ratio 12:3:1 for rough : intermediate-smooth : smooth

2 Segregating 3 rough : 1 intermediate-smooth

2 Segregating 3 rough : 1 smooth.

Intermediate-smooth awned plants:

1 breeding true for intermediate-smooth

2 segregating 3 intermediate-smooth : 1 smooth

Smooth awned plants:

Breeding true for smooth awn.

Three crosses involving Trebi and Glabron were given further study in the F_3.

The behavior of F_3 lines from plants classified as rough awned in the F_2 is given by the data in Table III.

TABLE III.

The behavior of F_3 lines from plants classified as rough awned in F_2, compared with the theoretical ratio 2:2:1:1.

Cross Number		Non-seg Act.	Non-seg Theor.	Seg.12:3:1 Act.	Seg.12:3:1 Theor.	Seg.3 rough: 1 int.-smooth Act.	Seg.3 rough: 1 int.-smooth Theor.	Seg.3 rough : 1 smooth Act.	Seg.3 rough : 1 smooth Theor.	X^2	P
Glabron x Trebi	12	63	47.67	29	47.67	32	23.83	19	23.83	15.960	0.001
Trebi x Glabron	21	24	26.67	25	26.67	17	13.33	14	13.33	1.42	0.71
Trebi x Glabron	45	39	36.00	33	36.00	22	18.00	14	18.00	2.28	0.52
Total of Crosses 21 & 45		63	62.67	58	62.67	39	31.33	28	31.33	2.58	0.47

The fits are remarkably close to the theoretical in crosses 21 and 45, but a wide deviation occurs in the case of cross 12. It will be seen that the homozygous rough awned lines are too numerous, whereas, those segregating in the ratio of 12:3:1 are too few in number. This poor fit is very difficult to explain as it would seem very unlikely that lines segregating for any degree of smoothness would be placed in the homozygous rough awned class. An examination of the data in Tables V, VI and VII shows that the ratios of segregating plants within the F_3 lines resulting from rough awned F_2 plants are quite normal.

The behavior of F_3 lines from plants classified as intermediate-smooth in the F_2 is supplied by the data given in Table IV.

TABLE IV.

The behavior of F_3 lines from plants classified as intermediate smooth awned, in F_2, compared with the theoretical ratio 1 : 2.

Cross	Number	Non-seg. Act.	Non-seg. Theor.	Seg. 3 int.-smooth : 1 smooth Act.	Seg. 3 int.-smooth : 1 smooth Theor.
Glabron x Trebi	12	19	13.66	22	27.32
Trebi x Glabron	21	7	7.00	14	14.00
Trebi x Glabron	45	13	9.00	14	18.00
Total		39	29.66	50	59.32

A very close fit to the expected is obtained in cross 21. Certain deviations occur in crosses 12 and 45 that can possibly be explained by the fact that when only small numbers of smooth awned plants occurred in segregating lines they were overlooked and classified as intermediate-smooth. Further evidence of the difficulties encountered in distinguishing these two types is supplied by the data in Table VIII, where it will be seen that the F_3 segregating lines derived from intermediate-smooth awned F_2 plants contain too many intermediate-smooth awned types at the expense of the smooth awned. This accounts for the poor fits to the theoretical obtained in these (~~in these~~) instances.

TABLE V.

Summary of the ratios of rough : intermediate-smooth : smooth awned plants in F_3 segregating lines, compared with the theoretical 12:3:1.

Cross	Number		Rough	Inter.-Smooth	Smooth	X^2	P
Glabron x Trebi	12	Act.	879	226	85	1.76	0.47
		Theor.	892.50	223.13	74.38		
Trebi x Glabron	21	Act.	800	182	70	1.61	0.46
		Theor.	789.00	197.25	67.25		
Trebi x Glabron	45	Act.	1014	258	89	0.27	>0.61
		Theor.	1020.75	255.19	85.06		

TABLE VI.

Summary of the ratios of rough : intermediate-smooth awned plants in F_3 segregating lines, compared with the theoretical 3:1.

Cross	Number		Rough	Inter.-Smooth	Dev. / P.E.	Odds
Glabron x Trebi	12	Act.	969	268	4.02	142.26:1
		Theor.	927.75	309.25		
Trebi x Glabron	21	Act.	551	165	1.77	3.45:1
		Theor.	537.00	179.00		
Trebi x Blabron	45	Act.	674	200	2.14	5.38:1
		Theor.	655.50	218.50		

TABLE VII.

Summary of the ratios of rough : smooth awned plants in F_3 segregating lines, compared with the theoretical 3:1.

Cross	Number		Rough	Smooth	Dev./P.E.	Odds
Glabron x Trebi	12	Act.	536	192	1.29	1.63:1
		Theor.	546.00	182.00		
Trebi x Glabron	21	Act.	445	146	less than 1	<1:1
		Theor.	443.25	147.75		
Trebi x Glabron	45	Act.	367	126	less than 1	<1:1
		Theor.	369.75	123.25		

TABLE VIII.

Summary of the ratios of intermediate-smooth to smooth awned plants in F_3 segregating lines compared with the theoretical 3:1.

Cross	Number		Inter.-Smooth	Smooth	Dev./P.E.	Odds
Glabron x Trebi	12	Act.	685	171	5.04	1350.35 : 1
		Theor.	642.00	214.00		
Trebi x Glabron	21	Act.	404	116	2.10	5.38 : 1
		Theor.	390.00	130.00		
Trebi x Glabron	45	Act.	447	102	5.15	1350.35 : 1
		Theor.	411.75	137.25		

It will be recalled that the F_2 material was originally classified into five classes. The data in Table IX show the distribution of the plants of the five F_2 groups on the basis of the breeding behavior in the F_3. Before discussing the data contained in this Table, it would be well to bring out the interesting observation that all the homozygous intermediate-smooth F_3 lines were composed of plants possessing awns having the characteristic smooth-base type of barbing, whereas, the segregating lines contained plants with both types of intermediate-smooth awns. This observation is supported by the data contained in Table IX. With reference to crosses 21 and 45 (cross 12 was not classified for the smooth-base type) it will be seen that the majority of the F_2 plants classified as smooth-base bred true, whereas, those F_2 plants classified as intermediate-smooth awned segregated. The data submitted, indicate that it is possible to separate the two genotypes rrSS and rrSs on the basis of their respective phenotypes. The factor S in homozygous condition causes a more pronounced type of barbing than it does in the heterozygous condition.

The data in Table IX also show the non-validity of the intermediate- rough class, since plants classified as such in F_2 behaved either as rough or as smooth base types. The F_3 behavior justifies the grouping adopted in the F_2.

It will be remembered that the F_2 material was origin-ally classified into five classes. The data in Table IX show the distribution of the plants of the five F_3 groups on the basis of the breeding behavior in the F_3. Before discussing the data contained in this Table, it would be well to bring out the interesting observation that all the homozygous intermediate-smooth F_3 lines were composed of plants possessing awns having the characteristic smooth-base type of barbing, whereas, the segregating lines con-tained plants with both types of intermediate-smooth awns. This observation is supported by the data contained in Table IX. With reference to crosses 21 and 45 (cross 12 was not classified for the smooth-base type) it will be seen that the majority of the F_2 plants classified as smooth-base bred true, whereas, those F_2 plants classified as intermediate-smooth awned segregated. The data submitted, indicate that it is possible to separate the two genotypes rrSS and rrSs on the basis of their respective phenotypes. The factor S in homozygous condition causes a more pronounced type of barbing than it does in the heterozygous condition.

The data in Table IX also show the [illegible] of the intermediate-rough class, [illegible] in F_3 behaved either as rough or as smooth [illegible]. The F_3 behavior justifies the grouping [illegible] in the F_2.

TABLE IX.

Distribution of the plants of the five original F_2 classes according to F_3 behavior.

F_3 behavior / F_2 class	Glabron x Trebi, Cross 12.					Trebi x Glabron, Cross 21					Trebi x Glabron, Cross 45				
	Rough	Int.-Rough	Smooth base	Int.-Smooth	Smooth	Rough	Int.-Rough	Smooth base	Int.-Smooth	Smooth	Rough	Int.-Rough	Smooth base	Int.-Smooth	Smooth
Rough	139		1			76					98			1	
Int.-Rough	1		5			4					8		3		
Smooth base	1							6	2		2		7	1	
Int.-Smooth			13	15				1	10				3	8	
Smooth				7	8				2	3				4	6
Total	141		19	22	8	80		7	14	3	108		13	14	6

A further study of the data in this table reveals the fact that a number of plants classified as smooth awned in the F_2 behaved as intermediate-smooth awned in the F_3. The actual ratios of the F_2 plants tested in the F_3, together with the corrected ratios, are given in Table X.

TABLE X.

Comparison of uncorrected and corrected F_2 ratios with the theoretical 12:3:1.

Cross	Number		Rough	Inter.-Smooth	Smooth	X^2	P
Glabron x Trebi	12	Uncorrect.	146	29	15	2.14	0.35
		Correct.	141	41	8	2.10	0.35
		Theor.	142.50	35.63	11.88		
Trebi x Glabron	21	Uncorrect.	80	19	5	0.09	very high
		Correct.	80	21	3	2.05	0.36
		Theor.	78.00	19.50	6.50		
Trebi x Glabron	45	Uncorrect.	109	22	10	1.90	0.39
		Correct.	108	27	6	1.39	0.51
		Theor.	105.75	26.44	8.81		
Total		Uncorrect.	335	70	30	2.04	0.36
		Correct.	329	89	17	4.73	0.10
		Theor.	326.25	81.56	27.19		

The individual crosses of the corrected F_2 data show satisfactory fits to the theoretical but as the number of smooth awned plants are low in all three cases the fit of the total is not so satisfactory.

The F_3 data presented, support rather well the original hypothesis that two factors explained on the basis of epistasis are involved in barbing of awn. The results are, therefore, in agreement with those reported by Griffee (12) and Robertson, Deming and Koonce (30).

It is interesting to note that the results of this study are not in agreement with those of David (7), who, as it has been stated, previously worked with the same cross as is discussed ~~used~~ in this paper. He reported that two-thirds of the progeny from smooth awned plants segregated in ratios approximating 3 smooth : 1 rough. No such inverse ratio occurred in the present work. It is possible that these two investigations have been carried out with different strains of barley known as Trebi. David describes Trebi as being "Six-rowed, white, high yielding, rough-awned variety ". It is not clear as to what sense he is using the word "white". If he is referring to the aleurone color, then he is definitely working with a different strain of Trebi than was employed in the present study. The aleurone color of the kernels of the Trebi parent used in this investigation was definitely bluish-grey. This description of the kernel color of Trebi is in accord with the description given by Harlan et al (43)

The individual crosses of the corrected F_2 data show satisfactory fits to the theoretical but as the number of smooth awned plants are low in all three cases the fit of the total is not so satisfactory.

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LENGTH OF RACHILLA HAIRS.

Literature review.

The short-haired rachilla is always covered with short, fine, woolly-like hairs, while the long-haired rachilla may be covered with either long, bristly, or long fine, hairs. Several investigators including Hor (20), Sigfusson (31), and Robertson (29) have reported a single pair of factors to be responsible for this character.

Method and experimental results.

In the present study by combining in one class all those plants having long-haired rachilla, regardless of type, a very excellent fit to a 3:1 ratio is obtained (Table XI).

TABLE XI.

Distribution of plants for rachilla hairs in the F_2 of reciprocal cross of Glabron x Trebi.

	long-haired rachilla	Short-haired rachilla	X^2	Odds
Act.	796	287	1.7	2.98 : 1
Theor.	812.25	270.75		

These data indicate a simple monohybrid inheritance with the long-haired condition dominant.

A Linkage Study.

Literature review.

It has been shown by a number of investigators that a linkage exists between the factor pair concerned in length of rachilla hairs and the main factor pair concerned in the barbing of awn. Sigfusson (31) and Robertson , et.al. (30), working with the repulsion phase report 30.8 and 34.63 ± 1.76 percent crossing over,respectively. Hor (20) obtained 28.70 ± 3.43 percent crossing over in the repulsion phase and 34.54 ± 2.89 in the coupling phase. (Only one factor was found to be responsible for rough awn in the material used by Hor.)

Methods and experimental results.

The data in Table XII show the F_2 segregation of long versus short-haired rachilla and rough versus smooth awn. A cursory examination of the data reveals the short-haired rachilla class to contain too many rough awned plants and not sufficient intermediate-smooth and smooth awned plants. The reverse is true in the case of the long-haired rachilla class. The data indicate a linkage between one of the factor pairs responsible for rough awn and the factor pair for length of rachilla hairs. Since rough awn want into the cross with short-haired rachilla and smooth awn with long-haired rachilla, the linkage is in the form of repulsion.

[illegible] long-haired condition [illegible].

A Linkage Study.

[illegible]

It has been shown by a number of investigators that a linkage exists between the factor pair concerned in length of rachilla hairs and the main factor pair concerned in the barbing of awn. Sigfusson (51) and Robertson, et.al. (40), working with the repulsion phase report 30.8 and 24.03±1.76 percent crossing over, respectively. Hor (30) obtained 23.70±1.43 percent crossing over in the repulsion phase and 14.[illegible] in the coupling phase. [illegible] to be responsible for rough awn in the material used by Hor.)

Methods and [illegible]

The data in Table XII show the F_2 segregation of long-versus short-haired rachilla and rough versus smooth awn. A cursory examination of the data reveals the short-haired rachilla class to contain too many rough awned plants and not sufficient intermediate-smooth and smooth awned plants. The reverse is true in the case of the long-haired rachilla class. The data indicate a linkage between one of the factor pairs responsible for rough awn and the factor pair for length of rachilla hairs. Since rough awn went into the cross with short-haired rachilla and smooth awn with long-haired rachilla, the linkage is in the form of repulsion.

TABLE XII.

Distribution of F_2 plants for length of rachilla hairs and barbing of awns, in reciprocal crosses Glabron x Trebi.

Long-haired rachilla			Short-haired rachilla			
Rough	Inter.-Smooth	Smooth	Rough	Inter.-Smooth	Smooth	
538	189	69	251	21	15	Obs.
597	149.25	49.75	215.77	53.94	17.98	Calculated on basis of 2 groups of 3 classes each
X = 24.14			X = 26.36			

(X = 49.33 when the intermediate-smooth and smooth awned classes are grouped, that is, calculated ratio based on a 9:3:3:1.)

If S, the factor for intermediate-smooth awn, is linked with the factor for short rachilla hairs, l, then the short-haired intermediate-smooth awned class should be in excess of the theoretical. However, data in Table XII show that this class, on the contrary, has too few individuals; thus indicating that the factor for short-haired rachilla must be linked with R, the factor responsible for rough awn. Furthermore, it can be seen that ratio of intermediate-smooth; smooth awn plants within the long - and short-haired rachilla classes respectively, is fairly close to the theoretical 3:1. This is additional evidence that the factor pair Ss is independent of the factor pair Ll for rachilla hair length. On this basis the intermediate-smooth awned and smooth awned classes may be grouped in

the calculation of linkage between R and 1. Using the (3:1) (3:1)ratio of Immer's Tables (21), a crossover percentage of 33.4 ± 1.7 was obtained. When the observed data were compared to the theoretical on the basis of 33.4 crossing-over a fair fit, indicated by a P value of 0.18 ,was obtained (Table XIII).

TABLE XIII.

Comparison of the observed distribution of F_2 plants for length of rachilla hairs and barbing of awn, with the calculated, on the basis of 33.4% crossing over.

Long-haired rachilla		Short-haired rachilla		
Rough	Int.-Smooth and Smooth	Rough	Int.-Smooth and Smooth	
538	258	251	36	Obs.
571.72	240.52	240.53	30.20	Calc.on basis of 33.4% crossing over.
	X^2 = 4.93		P = 0.18	

It may, therefore, be concluded that a linkage exists between the main factor for barbing of awn and the factor concerned in rachilla hair length with a crossingover percentage of 33.4 ± 1.7. These results are in close agreement with those of Sigfusson (31), Hor (20) and Robertson et.al. (30).

Earliness of Heading.

Literature review.

Harlan and Martini (16) in a study of earliness in F_1 barley hybrids found that the hybrids headed quite uniformly as compared to their respective parents. The average awn-emergence date tended to be intermediate between the respective parents. The earliness of many hybrid combinations of late varieties indicated that they contained many factors for earliness.

As a result of studying the F_3 lines of a cross between Guy Mayle x Canadian Thorpe Neatby (27) concluded that growth period was governed by three main factors. He arrived at his conclusions by estimating the number of lines containing plants of winter habit and by comparing the standard deviations of the individual lines with the average of that of the parents. When these three factors are in a homozygous recessive condition winter habit results. Canadian Thorpe was thought to carry 2 factors and Guy Mayle one.

Griffee (12) found that earliness was governed by a single factor difference with early heading dominant. A distribution table for date of heading of F_3 lines showed the lines to be of three kinds, viz., early, segregating, and late. These three types appeared in approximately 1:2:1 ratio.

David (7) studied the inheritance of earliness in the cross that is under discussion in this paper. The F_1 was earlier than either parent. When the F_2 plants were graphed on the basis of the number of days from planting to flowering, a ratio of nine early to seven late was obtained. A study of the F_3 lines on the basis of mean number of days from planting to flowering substantiated the view that two important complementary factors were involved in the inheritance of earliness.

Methods and experimental results.

Detailed studies on the earliness of heading were made on two F_3 populations of reciprocal crosses between Glabron and Trebi. The emergence of awn combined with the splitting of the sheath of the first spike was taken as the criterion of heading. The number of plants heading out in each line was recorded in 2-3 day intervals during the heading period. The distribution of each line was expressed as the number of days from emergence to heading, and from this the mean of each line for the number of days from emergence to heading was calculated. The relative earliness of the lines of seven other crosses were estimated by recording the date when 10 percent of the plants were headed.

A number of observations in the field are of interest. Transgressive segregation for earliness and lateness was observed; certain hybrid lines were completely headed before any plants of the parental rows had commenced and conversely other hybrid lines did not commence heading until

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Methods and experimental results.

Detailed studies on the earliness of heading were made on two F_3 populations of reciprocal crosses between Alaska and Trebi. The emergence of awn combined with the splitting of the sheath of the first spike was taken as the criterion of heading. The number of plants heading out in each line was recorded in 2-3 day intervals during the heading period. The distribution of each line was expressed as the number of days from emergence to heading, and from this the mean of each line for the number of days from emergence to heading was calculated. The relative earliness of the lines of seven other crosses were estimated by recording the date when 10 percent of the plants were headed.

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the parental rows were completely headed. The parental rows were about mid-season in date of heading with Glabron approximately 3 days later than Trebi. Considerable variation existed, not only within individual lines, but between different areas in the field. Cool rainy weather occurring at heading time delayed heading in a number of the late lines. Although it has been thought that considerable care had been exercised in selecting the soil for the two populations used in this study it was found that cross 21 lay in an unproductive area of soil. This was shown by the fact that the difference in date of heading and height between Trebi and Glabron tended to be minimized. Furthermore, the lines of this cross generally matured earlier than those of other crosses. Examination of a number of the plants showed foot-rot symptoms but it is difficult to say if the unproductiveness of this area is due entirely to this disease. For the above reasons cross 21, outside of showing certain general trends, will not be of great value in the study of earliness. Approximately thirty lines of cross 12 were omitted from this study owing to the fact that they were situated on another ~~bank~~ bed, the history of whose soil varied slightly from that upon which the remainder of the cross was growing.

The distribution of the parental rows and hybrid lines, for the mean number of days from emergence to heading, of crosses 12 and 21 are given in Table XIV. The data of cross 12 are also shown in graphical form in Figure II.

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The distribution of the parental rows and hybrid lines, for the mean number of days from seeding to heading, of crosses 12 and 21 are given in Table IV. The data of cross 12 are also shown in graphical form in Figure IV.

TABLE XIV.

Distribution of F_3 lines and parental rows according to the mean number of days from emergence to heading in reciprocal crosses of Trebi and Glabron.

Parent or cross	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	Mean	Coefficiant of variability
	Classes for number of days																										
Trebi									1	1	2	2	-	1	-	1										58.88	3.56±.60
Glabron												1	2	1	1	1	-	2								61.88	3.56±.60
Cross 12 Glabron x Trebi	1	1	-	2	7	6	8	11	20	22	20	7	10	6	12	6	6	4	4	2	1	1	3	-	1	58.47	7.37±.27
Trebi									2	1	1	1														57.30	2.11±.45
Glabron									2	-	1	2														57.60	2.35±.50
Cross 21 Trebi x Glabron			1	5	9	7	3	14	11	9	5	9	10	4	2	4	1	4	1	3	2					57.43	7.55±.35

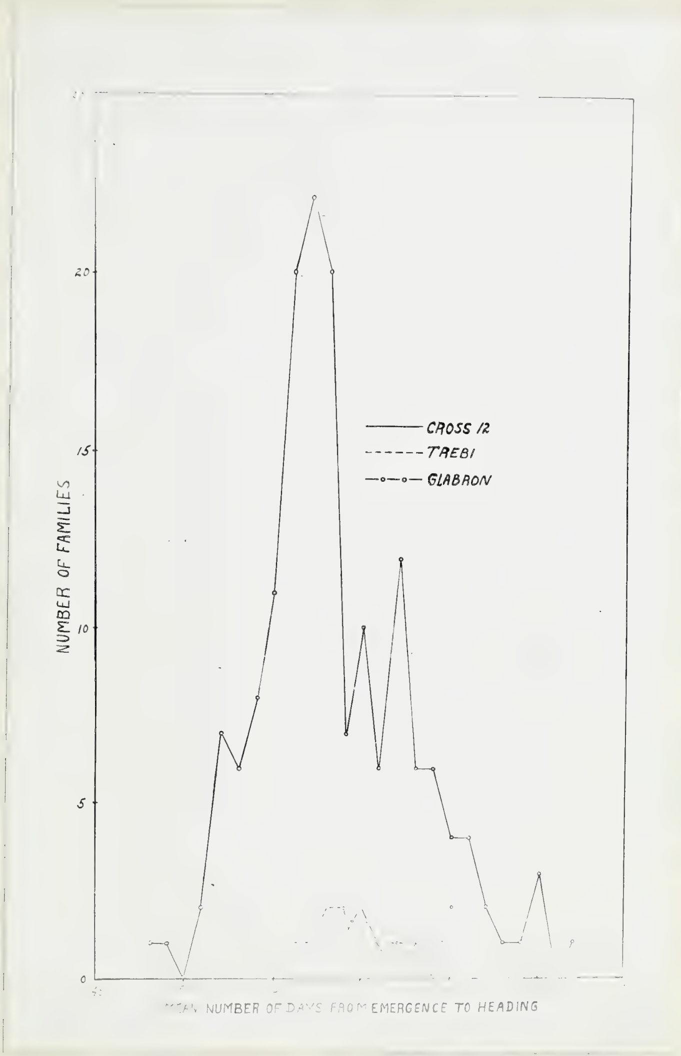

FIGURE II.

Curves showing distribution of F_3 lines and parental rows according to the mean number of days from date of emergence to heading in the cross Glabron x Trebi.

The distribution has been set out in daily intervals. Statistically, in view of the variability existing between the parental rows an interval of two days would be more accurate. The purpose in using the daily interval is an attempt to reflect as far as possible the distribution of the F_2 plants. David (7) was able to show that F_3 lines resulting from F_2 plants segregating 9:7 for early and late, were also in the ratio of 9 early : 7 late as judged by their means. A study of the curve in Figure II and the data in Table XIV reveals the fact that a distinct break occurs in cross 12 at 59 days and in cross 21 at 58 days. Using these points as an arbitrary dividing line, a good fit to 9:7 for early and late lines is obtained (Table XV).

TABLE XV.

Numbers of early and late F_3 lines as judged by their means as compared with the theoretical numbers on the basis of a 9 : 7 ratio.

Cross		Phenotypes	No.of lines Act.	Theor.	Dev.	Dev. / P.E.	Odds
Glabron x Trebi	12	Early	101	90.54			
		Late	60	70.42	10.42	2.45	9.89:1
Trebi x Glabron	21	Early	61	58.50			
		Late	43	45.50	2.50	0.73	<1:1

It was mentioned previously that the relative earliness of the lines of some seven crosses were determined by the date when 10 percent of the plants were headed. This method although of little value as far as early lines are concerned (as it takes no account of segregation for lateness) is of considerable value in the determination of the number of late lines. Estimations of the number of lines in each cross that were as late or later than the Glabron parent revealed the interesting fact that these constituted one-quarter of the total in each case. This would indicate that the late lines, comprising 7/10 of the whole, are made up of two groups: mid-late and late. This division of the late lines is not clearly shown by the curve in Figure II, although there is a suggestion of a second mode occurring around 61-62 days.

The data indicate that two main complementary factors are involved in earliness of heading. Trebi and Glabron have been found to occupy a more or less central position on the distribution surface with Glabron a few days later than Trebi in every instance. Assuming E and L to be the factors involved in earliness of heading, the only possible genotypes of the parents based on a two-factor hypothesis would be EEll and eeLL. A casual acquaintance with the F_2 genotypes of such a combination would show that the parental lines of both Trebi and Glabron, as judged by their mean, should fall to the right of the arbitrary divisional point. An examination of the parental curves

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in Figure II shows that the parents tend to be too early. This may be partially explained by the data given in Table XV where it will be seen that, judged by their means, the early hybrid lines tend to be too numerous. Apparently, environmental conditions were such as to encourage early heading.

David (7) was able to calculate the number of homozygous early and late lines by estimating the number of lines falling completely to the left or right of an arbitrary point, dividing the early lines from the late.

A study of the frequency distributions of the individual lines, in cross 12 of the work under discussion, showed 12 lines to fall completely to the left of the arbitrary divisional point of 59 days. Since 10 such lines would be expected from the population of 160 lines used, the number obtained appears quite significant. It was impossible to determine homozygosity in the late lines as cool rainy weather prolonged the heading period.

Another interesting observation arose from the study of the distribution of individual F_3 lines in this cross. Two lines were noticed to commence heading seven days after all others had started, and conversely three lines were found to have completed the greater portion of their heading when others were showing only a few plants. As these numbers roughly approximate 1/64 of the total population, it might be concluded that a third factor, working in conjunction with the two main complementary factors discussed above, was also involved in earliness of heading.

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A study of the frequency distributions of the individual lines, in cross 12 of the work under discussion, showed 12 lines to fall completely to the left of the arbitrary divisional point of 49 days. Since 10 such lines would be expected from the population of 160 lines used, the number obtained appears quite significant. It was impossible to determine homozygosity in the late lines as cool rainy weather prolonged the heading period.

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HEIGHT OF PLANT.

Literature review.

Vestergaard (40) reports a segregation of 14 dwarfs to 81 normal plants in the F_2 of a cross between Binder and a dwarf-like variant.

Miyake and Imai (25) crossed tall slim plants with short stout ones. The F_1 were tall and slim, whereas the F_2 segregated into a ratio of 3 tall to 1 short.

Miyayawa (26) found dwarfness tended to be dominant in a cross he studied. He also noted that the homozygous dwarfs were sterile. A segregation of one sterile dwarf to two dwarf to one normal plant was obtained in the F_2.

Harlan and Pope (14), on the other hand, found that a dwarf form behaved as a simple recessive to the normal barley.

Neatby (27) obtained height data on 228 F_3 lines of a cross between Guy Mayle and Canadian Thorpe. No clear indication of the number of factors involved was obtained. By comparing the standard deviations of the F_3 lines with those of the parents, Neatby concluded that at least four factors seemed to be operative.

David (7) studied plant height in all three generations of crosses between Glabron x Trebi and Velvet x Trebi. The F_1 in each cross were taller than the short parent and closely approached the height of the taller. The F_2 were much more variable than the F_1 and parental forms were

[illegible]

[illegible]

Vesterneerd (40) reports a segregation of 15 dwarfs to [illegible] normal plants in the F_2 of a cross between [illegible] and a [illegible]-like variety.

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Harlan and Pope (14), on the other hand, found that a dwarf form behaved as a simple recessive to the normal [illegible].

[illegible] (27) obtained height data on 232 F_3 lines of a cross between Guy Mayle and Canadian Thorpe. No clear indication of the number of factors involved was obtained. By comparing the standard deviations of the F_3 lines with those of the parents, [illegible] concluded that at least four factors seemed to be operative.

David (7) studied plant height in all three generations of crosses between Glabron x Trebi and [illegible] x Trebi. The F_1 in each cross were taller than the short parent and closely approached the height of the taller. The F_2 were much more variable than the F_1 and [illegible]

recovered in both the F_2 and F_3 generations.

Methods and experimental results.

The two reciprocal crosses used for the study of earliness also served as a basis for a study of plant height. The criterion of height was taken as the distance from the base of the culms to the tip of the spike, excluding awns. The plants were individually pulled and measured in inches. The variability noted in regard to earliness of heading was even more striking in the case of height of plant. Again the data obtained from cross 21 could not be used in the inheritance study.

The distribution of the mean heights of the progeny and parent rows of cross 12, together with their coefficients of variability are given in Table XVI.

TABLE XVI.

Distribution of hybrid lines and parent rows for mean height in inches, in the cross Glabron x Trebi.

Parent or cross	Mean height in inches.									Mean	C.V.
	29.5	31.5	33.5	35.5	37.5	39.5	41.5	43.5	45.5		
Trebi		1	5	1	1					34.00	4.88±0.82
Glabron						2	1	4	1	42.50	4.71±0.79
Glabron x Trebi 12	1	5	25	47	38	22	19	3	-	36.91	7.74±0.29

Trebi and Glabron will be seen to differ quite strikingly in height; Trebi being on the average eight inches shorter. The coefficient of variability of the F_3 lines, as compared to that of the parents, shows that the progeny are considerably more variable than the parental rows. This would indicate a segregation of genetic factors for height of plant if the numbers of parental rows were large enough to make any conclusions possible. Judged on the basis of their mean heights, the parental rows are seen to occupy the extremes of the distribution surface, while the distribution of the progeny approaches that of the normal. Cumulative factors would appear to be involved. Since height is a character readily affected by environmental factors, it is difficult to work out any definite mode of inheritance. It will be shown later that a positive correlation of approximately 0.73 exists between number of days to heading and plant height. Although this correlation may be partially explained on a physiological basis, its high value suggests that certain of the factors involved in earliness of heading are also concerned in the expression of plant height.

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Covered Smut Reaction.

The difficulty of obtaining satisfactory infections, combined with the early development of control measures, is largely responsible for the lack of genetic investigation on the covered smut disease.

Environmental relationships.

The only work of importance regarding the effects of environment on the development of the disease in the barley plant is supplied by Faris (8,9). Using controlled conditions he was able to obtain high infection percentages on Hannchen barley over wide ranges of soil temperatures and acidity and at moistures generally existing in the soil at the time of seeding. Soil temperatures varying from 10-25°C. with 40-50% moisture content gave good infections at pH values of 5,6,7 and 7.8. In general infection was influenced unfavourably by low soil temperature and moistures at time of seeding. Acid soils with both 40 and 50 percent moisture content gave higher infections than did slightly alkaline soils. The vigor of the host plant was found to have little or no effect on the development of covered smut, although the growth conditions following infection may have a marked effect in that regard. Faris also found that the character of the soil played an important role in obtaining satisfactory infections; quartz or builder's sand gave poor results while neutral potting soil gave normal infection.

Taylor and Zehner (35) have pointed out in the case of winter barley that greater infections resulted from deep seeding than from shallow.

The dehulled inoculated kernels used in the present inheritance study were seeded in ~~to~~ soil with a temperature of approximately 59° F. Owing to the rather dry nature of the surface soil, the seeds were planted a little deeper than had been originally planned.

Physiologic specialization.

Faris (8) emphasized the fact that one of the important requirements necessary to produce high infection was the use of inoculum collected from the variety on which it was to be tested. This suggested the presence of physiologic forms. In a later paper, (9), he demonstrated the presence of five forms using four varieties of barley as differentials.

The writer used a composite sample of smut spores collected from Trebi, Glabron, Velvet and Comfort, in all inoculations.

Dehulling studies.

A number of investigators have found that to obtain satisfactory infections of barley with U. hordei, dehulling of the kernel is necessary.

Tisdale (36) reports that in the case of winter barley the removal of the hull resulted in greatly increased infections. He removed the hulls by means of a scalpel and concluded that some simpler method of removing the hulls was

necessary if extensive smut tests were to be carried out.

Faris (9) also obtained greater infections when he used inoculated dehulled seed; but found that greatly reduced stands resulted. Examination of the unemerged seed showed that practically all the kernels had commenced germination but due to distortion few were able to reach the surface.

Briggs (1) reports extensive tests carried out at Davis, California, in the years 1919-21, with hulled seed of some 570 varieties and strains. Although the seeds were heavily inoculated with viable spores little infection resulted.

Barley covered smut tests carried out at the University of Alberta in the last three years, using hulled kernels, confirms the results reported by Briggs (1).

To obtain some simple method of dehulling the barley kernel, Briggs (1) studied the possibility of using sulphuric acid. It had been previously demonstrated that the seed coat of barley was surprisingly resistant to this chemical (2). In his investigations Briggs used many different combinations of concentration of acid and duration of treatment. The results he obtained are limited and consequently no definite conclusions can be drawn. Fortunately, the hull over the germ was found to be thicker than elsewhere, on the kernel and a thin covering often remained over the germ when the remainder of the kernel was completely dehulled. There appeared to be considerable variations in smut infection after apparently equal degrees of dehulling; due probably to the small numbers of plants used.

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Low concentrations of acid for a long period of time gave infections comparable to high concentrations for short periods of time. A certain amount of corrosion of the kernels was noted when the more concentrated acid was used. It was also observed that complete dehulling was not necessary for good infection; in fact a thin hull over the entire kernel seem to give better results. In general it may be said that this sulphuric acid method gave results comparing very favourably with seed dehulled by hand and offered a promising means of testing hybrid populations for smut reaction.

The method just described was utilized,in modified form, to dehull the kernels of the hybrid and parental lines used in the present inheritance studies. Since no conclusive evidence as to the optimum strength of acid and duration of treatment can be drawn from Briggs' investigation, and since there is ample room for further and special investigations in this regard, it was decided to use only the concentrated sulphuric acid.

Preliminary trials, not reported in this paper, showed that exposure to concentrated acid for a period of 4-5 minutes had little deleterious effect on the germination of kernels of Glabron and Trebi, the parents of the hybrids under study. In fact, a thin hull remained over the greater part of the kernel. To facilitate the treatment of the kernels of a large number of F_2 plants the apparatus shown in Figure III was devised.

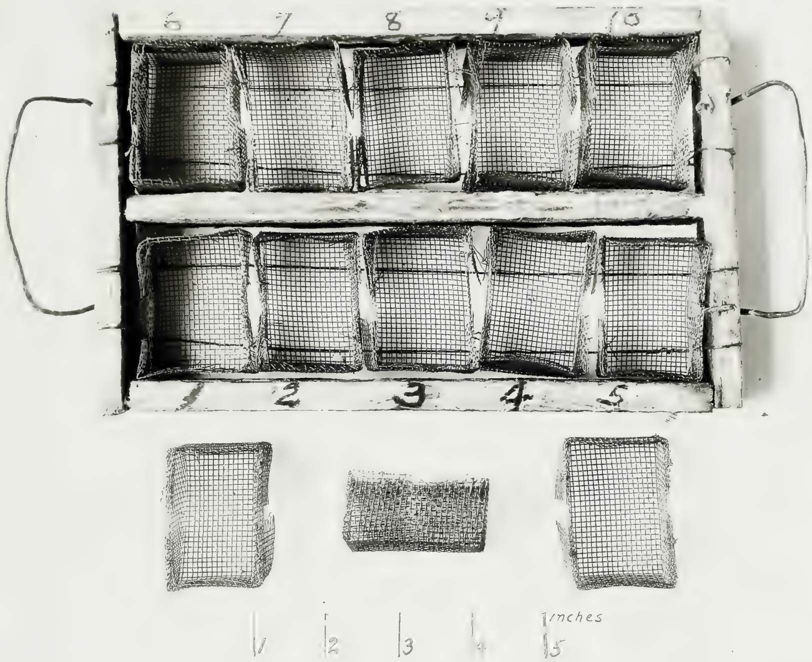

FIGURE III.

Immersion tray (including wire baskets) used in the dehulling of barley kernels by the sulphuric acid method.

This apparatus consists of a tray composed of a wooden frame coated with paraffin, and two strands of copper wire serving as a support for two rows of bronze netted-wire baskets. The identity of the latter is kept by a number found opposite them on the frame. The method utilized in dehulling the kernels of the parental materials will serve to illustrate the general technique adopted, while a modified method used in dehulling the kernels of the hybrid lines will be described later.

The number of the basket into which the kernels are placed is written on the envelope from which the kernels were taken, thus insuring that the identity of the sample will not be lost. The tray containing the ten samples is immersed in the concentrated acid for a period of approximately five minutes, then removed and plunged quickly into cold water. Here the kernels are washed vigorously for about two minutes. To counteract any acid that might still remain on the kernels the tray is immersed in a concentrated solution of $NaHCO_3$ (baking soda) for a period of 2-3 minutes. The kernels are then washed a second time before being placed on blotting paper to dry. After drying the samples are returned to their original envelopes.

After this treatment the majority of the kernels were found to be completely dehulled except for a thin hull remaining over the embryo.

During this operation it was found that if kernels which had been treated for a short time were washed in water and then returned to the acid for only a few seconds, rapid and

complete dehulling resulted. Germination tests run in the laboratory showed only slight reductions in germination of the treated kernels as compared to the normal. The degree of dehulling was as complete as that produced by the five minute method and the injury appeared to be less. The method appeared so promising in the light of the germination tests that it was decided to utilize it in the dehulling of the kernels of the hybrid lines. The technique of both methods was essentially the same except that in the modified method, the tray was removed from the acid after two minutes, washed with cold water, and replaced in the acid for the brief period of ten seconds.

A number of precautions had to be taken. Only five or six trays of kernels could be treated in one lot of acid as the digested portions of the hull rendered the acid less effective. It was also observed that when more than fifty kernels were placed in a basket less uniform results were obtained; certain of the kernels escaping normal treatment. Severely threshed kernels showed considerable corrosion ; the germ often being partially digested.

Criticism may be directed at this phase of the work in that different methods were used in dehulling the parental and the hybrid materials, respectively. Preliminary tests showed that the degree of dehulling and the amount of injury resulting from these two methods varied but slightly. Briggs (1) has pointed out that complete dehulling is not necessary for optimum infection. With this in mind it can be concluded that slight variations in the degree of

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dehulling will have little or no effect on the percentage of smut finally appearing on the plants ~~of~~ from such kernels.

As it has been pointed out previously the dehulled kernels were heavily inoculated with a composite sample of covered smut spores and seeded rather deeply ~~into~~ in soil of a temperature approximately 59°F. Unfortunately no rain fell for a period of 7-8 days following seeding. The emergence of the seedlings was very ununiform until the advent of rain after which a considerable number of seeds were stimulated to germinate. Notwithstanding this additional germination, a study of parental and hybrid lines showed disappointing results. Large unaccountable fluctuations occurred, for lines with only fifteen plants were bordered by lines containing thirty-five plants.

As the number of kernels sown per line was only approximated, the average percentage germination cannot be definitely given. A rough estimation would place the mortality between 40-50 percent.

The fluctuation in the parental rows was also very evident. Check rows of Glabron showed a germination range from 15-47 plants. Trebi exhibited even more variability due in part to the slower germination of the kernels thus allowing a greater opportunity for attack by mould fungi. Ten consecutive rows of Trebi (the contents of tray) showed very low germination percentages. This is difficult to explain when it was thought that identical treatment had been given each lot of kernels.

An examination of a number of the lines low in germination revealed the fact that in the majority of cases germination had commenced, but due to either the direct weakening effects of the acid or to the indirect effect of dehulling which predisposed the young seedlings to a number of adverse environmental factors, the seedlings ~~was~~ were unable to reach the soil surface. Faris (9) found the kernels dehulled by hand and inoculated with covered smut spores germinated normally but the seedlings were so distorted as to be unable to reach the soil surface. This is undoubtedly due to the creation of a more favourable condition for the smut fungus and a consequent greater infection of the young seedlings. A large number of the unemerged seedlings, examined in the present study, had made good progress in growth but due to extreme distortion had been unable to reach the soil surface (see Figure IVb). This would indicate that the failure to emerge in the case of these seedlings was due more to the greater opportunity of infection afforded the smut fungus than to any direct injury by the acid.

Other seedlings were found whose germination processes were early arrested by certain blue mould fungi. (See Figure IVc). It is highly probable that had environmental conditions been a little more favourable these seedlings would have evaded such fungi.

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FIGURE IV.

Injured barley seedlings, resulting from kernels dehulled by sulphuric acid and followed by inoculation with the spores of Ustilago hordei.

A. Healthy seedlings resulting from non-dehulled uninoculated kernels.
B. Distorted seedlings resulting from dehulled, inoculated kernels.
C. Seedlings from kernels treated identically with B, showing distortion and stunting as a result of attack by mould fungi shortly after germination.

Unfortunately, no dehulled uninoculated rows were seeded, so that it is impossible to state just what proportion of the injury is due to the acid and what proportion is due to severe infection by the smut fungus. Since no infection occurred in the loose smut nursery, it would seem that a comparison of the duplicate lines in these nurseries might throw some light on the problem. It has already been mentioned that the number of kernels sown for each line ~~were~~ was only approximated. This difficulty, combined with the fact that owing to contamination of the loose smut inoculum scattered infection with covered smut, occurred; a direct comparison is not possible. A study of duplicate lines in the two nurseries revealed a general parallelism in the degree of injury. However, here again great variations occurred.

The kernels of a number of standard varieties were dehulled by the method outlined for the hybrid lines. Certain differences were noted in the amount of dehulling occurring between those varieties. The field germination together with the infection percentages for each variety ~~is~~ are given in Table XVII.

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TABLE XVII.

Percentage germination and infection with covered smut in 29 varieties of barley grown from seed treated with concentrated sulphuric acid, and inoculated with spores of *U.hordei*.

Variety	* N.S.N.	No.of Plants	No. infect-ed	% infect-ed
Trebi	I-27-7	36	9	25.0
O.A.C.	I-29-3	42	1	2.4
Bearer	I-27-6	23	2	8.7
Star	I-30-3	10	2	20.0
Manchurian	I-0-1	29	16	55.2
Minsturdi	I-28-16	26	2	7.7
Peatland	I-28-18	17	4	23.5
Legal	I-29-2	42	7	16.7
Sacremento	I-31-1	10	0	0.0
Vaughn	I-31-3	29	6	20.7
Olli	I-32-2	32	6	18.8
Colsess	I-29-1	35	3	8.6
Sol	I-31-5	16	2	12.5
Glabron	I-28-15	38	0	0.0
Velvet	I-28-35	36	1	2.8
Comfort	I-30-2	41	4	9.8
Wis. Ped. 38	I-31-1	23	2	8.7
Harrington Sel.	I-25-5	9	0	0.0
265 x O.A.C.21	H-19-146	25	7	25.9
Canadian Thorpe	I-0-3	14	1	7.1
" " (decid.)	S-29-2	30	0	0.0
Horn	I-27-4	48	1	2.1
Charlottetown	I-27-2	20	9	45.0

Table XVII (Continued).

Variety	N.S.N.*	No.of plants	No. infect-ed	% infect-ed
Hannchen	I-27-1	14	5	35.7
Duckbill	I-30-5	10	3	30.0
Gold	I-28-5	9	1	11.1
Alberta Beardless	S-29-1	12	1	8.3
Success	I-32-4	26	0	0.0
Spartan	I-28-20	15	2	13.3

* Nursery stock number.

The data presented in the above table would indicate that definite differences exist in the ability of the kernels of certain varieties to germinate after acid treatment. Since the kernels of some varieties were more susceptible to threshing injury than were others, it is difficult to say whether the injury was due to a greater susceptibility of the hull to acid, or to the embryos of the kernels being unprotected. The great reduction in germination of the kernels of two varieties of barley, after treatment with acid and inoculated with spores of U. hordei, is shown in Figure V. The retardation of growth of the plants from treated kernels is also quite evident. Figure VI shows certain apparent varietal differences in the ability of barley kernels to germinate after acid treatment and inoculation with spores of U. hordei.

FIGURE V.

Effects of dehulling the kernels of two varieties of barley with H_2SO_4, followed by inoculation with the spores of U. hordei, upon emergence and vigor of growth of the barley seedlings.
Left to right:
Colsess - hulled, uninoculated.
Colsess - dehulled, inoculated.
Spartan - hulled, uninoculated.
Spartan - dehulled, inoculated.
Eureka - naturally hulless, uninoculated.

(Note the stunting effect of the acid on the plants in the treated rows).

FIGURE VI.

The effects upon the germination of kernels of four varieties of barley, when dehulled by acid and inoculated with spores of Ustilago hordei.

Five central rows, left to right:

New Era - naturally hulless.
Olli - dehulled by acid.
Vaughn - dehulled by acid.
Sacremento - dehulled by acid.
Regal - dehulled by acid.

In an endeavor to determine just what factors were responsible for the lack of emergence noted in dehulled inoculated lines, a number of greenhouse experiments were conducted. The modified acid treatment was used on several varieties. Certain minor variations between varieties will be observed but owing to the small number of kernels used, only totals or averages will show reliable trends. An experiment was outlined in an attempt to find out whether or not the reduction in germination could be explained in part by the greater opportunity of infection afforded the pathogene by the dehulled seed. For this purpose uninoculated and inoculated lots of normal kernels, kernels dehulled by hand and kernels dehulled by acid, were seeded in unsterilized soil. The results are laid out in Table XVIII.

Two conclusions may be drawn. In the first place kernels dehulled by acid gave much lower germination than kernels dehulled by hand. In the second place, whereas there is no difference in the percentage germination of uninoculated and inoculated, hulled kernels; there is considerable difference in this regard, in the dehulled lots. This fact is especially significant in case of the kernels dehulled by hand, and would indicate that reduction in germination of dehulled inoculated kernels is due in part to the severe infection of the seedlings by the pathogene.

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TABLE XVIII.

Percent germination of 5 varieties of barley hulled, dehulled by hand, and by H_2SO_4 when inoculated with spores of *Ustilago hordei*.

Variety	Normal hulled		Dehulled by hand		Dehulled by acid(mod.)	
	Uninoc.	Inoc.	Uninoc.	Inoc.	Uninoc.	Inoc.
	% germ.	% germ.	% germ.	% germ.	% germ.	% germ.
Glabron	93.3	80.0	90.0	76.7	50.0	40.0
Trebi	86.7	86.7	83.3	80.0	43.3	33.3
Bearer	90.0	90.0	100.0	80.0	60.0	53.3
Harrington Sel. I-25-5	86.7	80.0	96.7	63.3	30.0	20.0
O.A.C. No.21	93.3	96.7	66.7	46.7	33.3	23.3
Average	88.0	86.7	87.3	69.3	43.3	36.6

As blue mould fungi were found to be complicating the results in the field; it was decided to run a test on both sterilized and unsterilized soils. In this experiment uninoculated and inoculated lots of both hulled and acid-dehulled kernels were used. The results as summarized in Table XIX show that the uninoculated and inoculated hulled kernels germinated equally well ~~on~~ in both sterilized and unsterilized soil.

TABLE XIX.

Germination of H_2SO_4 dehulled kernels of 7 varieties of barley when inoculated with spores of *Ustilago hordei* and sown in sterilized and unsterilized soil.

Variety	Sterilized Soil				Unsterilized Soil			
	Hulled		Dehulled		Hulled		Dehulled	
	Uninoc.	Inoc.	Uninoc.	Inoc.	Uninoc.	Inoc.	Uninoc.	Inoc.
O.A.C.No.21	12	14	8	8	15	13	13	6
Hannchen	12	14	10.	8	14	13	6	1
Trebi	13	13	8	7	14	13	9	3
Canadian Thorpe	12	14	5	5	12	12	2	4
Peatland	14	14	12	11	11	13	5	2
Gold	15	12	8	8	14	14	9	7
Glabron	15	12	4	4	15	15	3	1
Total germination	95	93	55	51	95	93	47	24

There is a greater reduction in germination from dehulled kernels (both uninoculated and inoculated) when grown on unsterilized soil than when grown on sterilized. Probably the most striking fact shown by the data in Table XIX is that , whereas the dehulled uninoculated and inoculated kernels show little difference in germination on sterilized soil, they exhibit quite a marked difference in this regard on unsterilized soil; the inoculated kernels being much lower in germination. This is difficult to explain unless it is assumed that conditions existing in the unsterilized soil favour severe infection of the barley seedling by the pathogene.

The injury resulting from treating severely threshed kernels is plainly evident from the data given in Table XX.

TABLE XX.

Percent germination of severely threshed kernels of 4 varieties of barley when treated with H_2SO_4.

Variety	Random sample		Severely threshed	
	Non-treated	Treated	Non-treated	Treated
	% germ.	% germ.	% germ.	% germ.
O.A. C. No.21	93.3	63.3	86.7	0.0
Canadian Thorpe	93.3	43.3	83.3	0.0
Wisconsin Pedigree No.38	100.0	90.0	93.3	0.0
Harrington Sel. I-25-5	100.0	50.0	53.3	3.3
Average	96.7	61.7	79.2	0.8

The kernels described as "severely threshed" were made up of only those individuals showing a split or break of the hull over the embryo; no completely dehulled kernels being treated.

Summarizing the dehulling experiments briefly, it may be said that unaccountable fluctuations in field germination resulted from what appeared to be equal degrees of acid treatment. Field and greenhouse observations show a number of factors to be concerned in reduction of germination. The direct inability of the kernels to withstand the acid treatment is doubtlessly an important factor. Almost as important

is the practice of treating kernels exhibiting mechanical damage. After seeding, the attack by certain blue mould fungi, as well as increased infection by the pathogene, are instrumental in reducing the number of plants reaching the soil surface.

Genetic studies.

As far as the writer is aware no work of a genetic nature has appeared in the literature.

In the study to be reported the reactions of the lines of nine crosses, involving Glabron and Trebi, to the covered smut disease were determined. Considerable variation in the severity of infection of individual plants was noted (Figure VII). This was due to the fact that the first spikes to emerge from the sheath tended to escape infection. Infected culms were found to be slower in heading than the healthy ones, and in some cases the smutted spikes, rather than pushing their way through the top of the sheath, simply forced their way through the base. In one or two cases the peduncle bearing the smutted spike was badly distorted (Figure VII). In no cases did the leaves show smut pustules as was observed by Faris (8) in the case of severely infected plants.

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FIGURE VII.

Barley plants infected with covered smut, Ustilago hordei.

Left to right:

Normal plant.

Totally smutted plant, with the spikes just emerging from the sheaths. (Note the distortion of the peduncle).

Totally smutted plant, with spikes fully emerged.

Partially smutted plant, showing one normal spike and one smutted only at the base.

All plants exhibiting any degree of infection were called susceptible. The percentage infection was calculated for all lines containing fifteen or more plants and the lines were grouped in classes according to the percentage infection. A class interval of 10 percent was used. A zero class was added to include all lines showing no infection.

The reaction of F_3 lines and parental varieties to the covered smut disease is supplied by the data given in Table XXI. The Glabron parent appears highly resistant while the Trebi may be classed as moderately susceptible. The wide range of infection percentages exhibited by the Trebi parent would indicate that infection had not been altogether satisfactory. With this fact in mind, it is not altogether surprising that the hybrids do not lend themselves to factorial analysis. The progeny exhibit high resistance; there being little evidence of transgression toward greater susceptibility.

TABLE XXI.

Reaction of F_3 lines and parental varieties to *Ustilago hordei* in reciprocal crosses of Glabron and Trebi.

Parent or cross		Infection classes in percentage						
		0	5	15	25	35	45	55
Trebi		-	2	11	8	4	2	-
Glabron		9	24	2	-	-	-	-
Glabron x Trebi	6	2	14	10	6	1	1	-
	11	-	8	29	18	11	3	-
	12	13	49	37	10	6	3	2
	13	22	33	22	14	3	2	1
Trebi x Glabron	19	2	21	10	7	6	4	1
	20	4	11	24	10	8	4	1
	21	-	15	13	14	12	3	3
	23	-	6	11	17	10	9	1
	45	20	17	24	7	1	1	-
Total		63	174	180	103	58	30	9

Loose Smut Reaction.

The method of seed inoculation discovered by Tisdale and Tapke (37) to induce infection with *U. nuda* was used in the present investigation. Complete failure of infection resulted. Tapke (34) has recently reported the occurrence of a new species of loose smut, *Ustilago nigra*, capable of producing seedling infection. The spores of this fungus are not only larger and darker in colour than those of *U. nuda* but retain their viability over a much longer period of time. Examination of the inoculum used in the present study, revealed spores typical of *U. nuda*. This ~~would~~ might explain the lack of infection reported above. Vanderwalle (38) showed the existence in loose smut of a particular late type which he considers to be intermediate between *U. nuda* and *U. hordei*.

It is apparent in the light of these recent findings that comparatively little is known regarding the etiology of the loose smut ~~fungus~~ disease. Further investigation in this regard is imperative if extensive breeding programmes for resistance to this disease are to be carried out.

Stripe Reaction.

H. gramineum, the causal agent of the barley stripe disease, does not readily produce conidia on artificial media. ~~is considered an obligate parasite, since few authentic records exist to show that it has produced conidia on artificial media.~~ For this reason, difficulty may be experienced in obtaining sufficient inoculum for extensive breeding tests. The disease has always been interesting because the pathogene was supposed to infect plants at flowering time and to cause a systemic infection similar to that of loose smut of wheat and barley. Several studies regarding the mode of infection of this fungus have modified the views in this regard.

Method of infection.

Ravn (28) concluded that H. gramineum, like certain smut fungi, inhabits the growing point of the host plant and thence spreads to each young part of the plant during the formation of that part. He found that the bulk of the infection occurred at flowering time and that low percentages of infection occurred when germinated seedlings were grown in the presence of mycelium.

Vogt (41) as a result of histological studies showed the mycelium inhabited the space between the glumes and the pericarp and is never found in the embryo or in the endosperm. Infection was found to take place through the coleoptile rather than the embryo.

[illegible]

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Smith (32) came to similar conclusions in that he found infection to occur while the shoot is still under the adherent glumes or during its emergence. The inoculum was found to comprise, (a) conidia lodging at the awn end of the grain, (b) mycelium penetrating from the glumes and (c) perithecia formed inside or outside the glumes.

Johnson (23) showed that it was possible to obtain artificial infection of barley by simply inoculating the germinating kernels with spores or mycelia. Dehulling of the kernel increased the infection considerably.

In a later paper, Smith (33) showed definitely how infection of barley seedlings takes place. Mycelium is considered to be the main source of inoculum and is capable of living for at least two years in the chaff and pericarp. On the germination of the kernel the hyphae infect the primary sheaths, the coleorhiza (leading to root decay) and the coleoptile (causing leaf disease). From the coleoptile each successive leaf as formed is infected - the lesions on the newly infected leaf paralleling those on the older leaves enclosing it. The uppermost infected leaf may cause external infection of the young spike. Thus it can be seen that the mode of infection is contrary to that of smut infection. That is to say, the leaves are infected first and the growing point later, whereas, in the smuts the growing point is first infected and the other parts attacked as they are formed.

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Temperature relationships.

Several investigators have demonstrated that low soil temperatures favour infection of barley seedlings with H. gramineum.

Ravn (28) found that early planting produced greater infection. Johnson (23) showed, by the use of controlled experiments, that low soil temperatures are favourable to increased infections. He found the optimum temperature to be 10 - 12 ^{o} C., while little occurred at soil temperatures higher than 20^{o} C. Smith (33) points out that low soil temperatures greatly slow down germination processes, thus increasing the likelihood of infection while the shoot is still confined within the chaff. It has been noticed that barley growers in western Canada ~~the West~~ are troubled very little with damage from the stripe disease, whereas, considerable injury occurs in the barley plots at the experimental stations. The probable explanation,is that, in view of the fact that barley is generally seeded much later in ordinary farming practice than it is at the experimental stations, the high temperatures inhibit development of the fungus.

In the present study the inoculated kernels were planted as early in the spring of 1932 as was deemed practible, with soil temperatures ranging about 50^{o}-55^{o} F.

Physiologic specialization.

Physiologic specialization in this fungus was first demonstrated by Johnson (23). A single spore isolation obtained from Edmonton, Alberta, failed to recover when kept at 32°-33° C. for 10-12 days, while several other cultures tested in a similar manner recovered and grew normally. This form also grew better at 5-6° C. than did the other cultures under test.

Christensen and Graham (4) found 84 culturally distinct forms on testing 226 monosporous cultures obtained from United States, Canada and Germany. The pathogenicity of 75 races tested on several varieties of barley showed additional evidences of specialization.

Isenbeck (22) reports that American forms of this fungus were less virulent than the German. Differences in pathogenicity of the forms were noted.

Inoculation methods.

It has been shown that the source of primary infection is the presence of mycelium (or conidia) either in the pericarp or lodged between the pericarp and kernel. Mention has been made that Ravn (28) obtained good infection by floral inoculation of barley plants, while high infections were obtained by Johnson (23) when dehulled germinating kernels were inoculated with either the spores or mycelia. The period of greatest susceptibility in dehulled kernels, according to Johnson, appeared to be just subsequent to the emergence of the coleoptile.

Genau (11) found the optimum time to inoculate to effect floral ~~inoculation~~ infection with conidial suspension was the day following opening, provided the temperature approximated 25° C. Young seedlings 1-2 cm. in height were found to be readily infected by means of a conidial suspension in sufficiently warm and humid atmospheres. In one experiment the plants were successfully inoculated with the ascospores of the fungus.

Fuchs (10) has devised a method of artificial inoculation consisting of the injection of a conidial suspension of the fungus into the ripe grain after soaking the latter for an hour or two in water so as to loosen the glumes from the grain and permit of inserting the needle between them. For large quantities of inoculum a modified method was devised. The barley grains were placed in a vacuum for 20 minutes in a conidial suspension in such a way that the air between the glumes and seed is removed. When the pressure is restored the conidial suspension penetrates with great impetus between the glume and the caryopsis. To stimulate abundant mycelial production, the inoculated grains are placed in an incubator at temperatures of 25°C.-28°C. and at an atmospheric humidity of 90-100%. It is claimed that this method gave results in complete agreement with the floral method used by Genau(11).

Isenbeck (22) in a breeding study used methods of wet and dry flower infections, seedling infection and grain infection with spores or mycelia.

A method of floral inoculation, using a wet conidial suspension, was utilized in the present work. The inoculum consisted, in the main, of spores from diseased leaves from plants of a badly infected plot of Canadian Thorpe; this was supplemented from time to time by a composite sample of inoculum from the varietal plots. The infected leaves were placed in an incubating chamber over night to stimulate spore production. The following day the leaves were rubbed together under water until nothing but a pulp remained of them. The spore suspension was then strained through three layers of cheese-cloth to remove all suspended vegetative matter. Two heads from approximately 500 F_2 plants of crosses involving Trebi and Glabron, as well as two heads of 100 parental plants were selected at random for inoculation. This consisted of simply soaking the spikes with the solution and immediately enclosing them in a glassine bag. The heads were given additional sprays at four to five day intervals by means of an atomizer, the nozzle of the latter being inserted through a slit cut in the glassine bag. The weak straw of the barley plant caused considerable difficulty in that it was necessary to support the majority of the bagged spikes. Even with this precaution a number of spikes were broken over by the wind and rain.

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Genetic studies.

The only work to appear in the literature regarding the inheritance of reaction of barley to *H. gramineum* is that reported by Isenbeck (22). The progeny of 8 crosses with different combinations of immunity, resistance and susceptibility in the parents were studied. The F_2 flowers were inoculated thus giving ratios for the F_3. The F_4 was also studied in some cases. All the crosses were tested by the method of wet infection, two by dry infection and one F_3 was also tested in the greenhouse by the infection of the grain. Generally immunity was found to be dominant; crosses between two immune varieties gave no susceptibles, whereas crosses between two resistant types resulted in some susceptible types. Transgression also occurred when two susceptibles were crossed. The results can be only explained by assuming a large number of factors.

It has already been stated that the inoculated seeds of the present investigation were seeded as early as possible to take advantage of the low prevailing soil temperatures. The infected plants showed characteristic symptoms of the disease; these showing up strikingly just prior to heading. Little or no partial infection occurred, the plants being ruined economically (Figure VIII). The infection classes, in percentage, for the parental rows and hybrid lines are given in Table XXII.

FIGURE VIII.

Barley plants infected with stripe, Helminthosporium gramineum. Normal plant in the centre.

(Photograph taken when normal plants were approaching maturity).

TABLE XXII.

Reaction of F_3 lines and parental varieties to <u>H. gramineum</u> in reciprocal crosses of Glabron and Trebi.

Cross or parent	Infection classes in percentage. 0	2.5	7.5	12.5	17.5	22.5	27.5	32.5	57.5
Trebi	39	8							
Glabron		8	14	12	7	5	1		
126 lines Glabron x Trebi	36	40	31	13	3	-	1	1	1
336 lines Trebi x Glabron	137	93	48	20	11	5	1	-	-
Total 462 lines	173	133	79	33	14	5	2	1	1

The Trebi parent appears to be highly resistant to the form of the pathogene <u>H. gramineum</u> used, while Glabron shows infection varying from 2.5 percent to 27.5 percent; with greatest number of lines showing from 7.5 to 12.5 percent infection. This wide range of infection percent exhibited by Glabron would indicate certain limitations in the inoculation methods employed. There is no evidence of any transgression toward greater susceptibility in the hybrids except in one line, which gave 57.5 percent infection. No particular significance can be attached to this line since there is no evidence that it did not result from an admixture. Isenbeck (22) found that the number of resistant individuals in the progeny increased with the degree of resistance of the two parents. The present results bear out this conclusion. Keeping the parental types

in view it is extremely difficult to postulate any definite mode of inheritance. It is important to point out, at this time, that the plants selected in the F_2 for inoculation were really a random distribution of the early plants, since there had been a tendency to select early plants for inoculation purposes. Whether or not this factor would have any effect on the percentage of infection obtained is open to question. Isenbeck (22) found that the early varieties tended to be more susceptible than the late.

The writer would like to suggest at this time that some method other than floral inoculation should be utilized if uniform results, so important to inheritance studies, are to be obtained. The element of chance plays such an important role in this type of inoculation that there is no certainty as to what percentage of the kernels of a spike will be successfully infected. Even the excellent precaution of bagging the heads, has a very decided weakness, in that the barley peduncle is not sufficiently strong to support these bags under any type of adverse conditions. It is doubtful whether the mycelium of the fungus develops normally on the spikelets of broken-over heads. Some method of inoculating the seedling or the mature kernel as pointed out by Genau (11) and Fuchs (10) seems more promising. Isenbeck (22) claims that for ordinary purposes and varietal trials, field infection was preferable, but for inheritance tests the greenhouse infection was better, in that it gave a more uniform and severe infection.

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CORRELATION STUDIES.

General

The importance of correlation studies cannot be over estimated when used in connection with the inheritance of disease reaction. This type of inheritance does not lend itself readily to factorial analysis, and it is only through establishing certain associations between the factors concerned in resistance and susceptibility, with those of some easily distinguishable morphological character, that it is possible to determine the number of factors concerned in a given disease reaction.

Griffee demonstrated in a striking manner the value of such linkage studies. He was able to show, by studying the reaction of F_3 lines to H. sativum in relation to three other independently inherited characters, that at least three factors were concerned in a certain type of resistance.

Characters correlated.

In this paper correlations were calculated between the different characters studied earlier. Since the data of all the characters, with the exception of barbing of awn, were in definite numerical classes, it was possible to use the correlation coefficient in the majority of cases.

Whenever the character of barbing of awn was involved, the correlation ratio was employed. Probable errors were computed by standard formulae (3,19).

The data in Table XXIII show a summary of the correlation values derived in the course of the inheritance studies just reported.

It will be seen that, with the exception of three, (marked by asterisks), the correlation values are significant in the light of their probable errors. High correlations exist between height and number of days to heading. It has already been explained in connection with inheritance studies on plant height, that, although this association may be partially explained on a physiological basis, its high value would suggest that certain genetic factors, responsible for earliness of heading, are also responsible for height of plant. Positive correlations exist between covered smut reaction and both mean number of days to heading and mean height of plant. These associations may also be explained on a physiological basis. The later lines allow for a more optimum development of the pathogene, and since height of plant and number of days to heading are highly correlated, the tall plants tend to show greater susceptibility. It should be remembered that height of plant entered the cross together with resistance to covered smut disease, hence no genetic linkage can be said to exist.

TABLE XXIII.

Correlation of characters in the F_3 hybrids of reciprocal crosses between Glabrön and Trebi.

Character and reaction correlated	F_3 hybrids	Correlation coefficient	Correlation ratio
		r	η
Mean height and mean number of days to heading	Cross 12	0.728±.025	
	Cross 21	0.737±.030	
Mean height and stripe infection	Cross 12 & 21	0.388±.112	
Mean height and covered smut infection	Cross 12	0.266±.060	
	Cross 21	0.498±0.65	
Mean number of days to heading and stripe infection	Cross 12 & 21	0.124±.130*	
Mean number of days to heading and covered smut infection	Cross 12	0.193±.059	
	Cross 21	0.366±.075	
Barbing of awn and mean height	Cross 12		0.211±.051
	Cross 21		0.084±.065*
Barbing of awn and stripe infection	Cross 12 & 21		0.292±.091
Barbing of awn and covered smut infection	Cross 12 21 & 45		.030±.043*

* Correlation values not significant.

Small positive correlations exist between the different combinations of stripe reaction, height of plant and smoothness of awn. Since smooth awn entered the cross, with height and resistance to the stripe disease, slight genetic linkages may be indicated. The low values of η obtained between barbing of awn and both plant height and reaction to the stripe disease render these associations very uncertain as to their statistical significance.

No significant correlations existed between mean number of days to heading and stripe infection; barbing of awns and covered smut infection, and between barbing of awn and mean height (one cross only).

ECONOMIC SIGNIFICANCE.

Selections from the F_3 hybrid lines were made on the basis of barbing of awn, disease resistance, earliness of plant maturity and strength of straw. Approximately 350 smooth-awned plant selections have been prepared for further testing in the F_4. In addition, seven homozygous F_3 smooth awned lines have been bulked for immediate rod-row yield tests.

SUMMARY.

1. Reciprocal crosses between Glabron and Trebi have been used to determine the inheritance of the following character pairs: Rough vs. smooth awn, long- vs. short-haired rachilla, early vs. late heading, tall vs. short and resistance vs. susceptibility to both U. hordei and H. gramineum. The character pair, rough vs. smooth awn was studied in the F_1, F_2 and F_3; the character pair long- vs. short-haired rachilla in the F_2 and the remaining character pairs in the F_3.

Studies on barbing of awn were also made in the F_2 of crosses involving Velvet and Trebi.

2. F_2 and F_3 studies showed the rough awned condition to be governed by two factors, which may be explained on the basis of epistasis. The factor R produces rough awn, while the factor S is hypostatic to R, and in the absence of R, produces the intermediate-smooth awn. The double recessive rrss produces the smooth awn. The phenotypes rough, intermediate-smooth and smooth were obtained in a 12:3:1 ratio in the F_2. The homozygous intermediate-smooth plants rrSS exhibited a stronger degree of barbing than did the heterozygous plants rrSs.

3. The factor pair long- vs. short-haired rachilla was shown to be inherited in a simple Mendelian manner.

4. A linkage was obtained between the factor pair responsible for rachilla hair length and the main factor pair for barbing of awn, the cross over value being 33.4 ± 1.7 percent.

5. Two main complementary factors were found to be involved in earliness of heading. There was a suggestion that a third factor pair might be operative.

6. The number of factors concerned in the inheritance of height is not clear. Parental forms were recovered and cumulative factors are indicated.

7. Kernels of parental and hybrid lines dehulled with concentrated sulphuric acid to induce greater covered smut infection, gave greatly reduced germination. Treating of severely threshed kernels was found to seriously impair the germination of such seeds. Many weakened seedlings resulting from acid-dehulled kernels were predisposed to attack by certain blue mould fungi. The greater opportunity of infection afforded the pathogene, resulted in great distortion of the seedlings, accompanied by failure to reach the soil surface.

8. No genetic hypothesis can be advanced for the inheritance of reaction to _U. hordei_. The Glabron parent showed relatively high resistance to the form of the pathogene used, while Trebi appeared to be moderately susceptible. Considerable variability existed in the infection percentages

4. A linkage was obtained between the factor pair responsible for rachilla hair length and the main factor pair for barbing of awn, the cross over value being 38.4±1.7 per-cent.

5. Two main complementary factors were found to be involved in earliness of heading. There was a suggestion that a third factor pair might be operative.

6. The number of factors concerned in the inheritance of height is not clear. Parental forms were recovered and cumulative factors are indicated.

7. Kernels of parental and hybrid lines dehulled with concentrated sulphuric acid to induce greater covered smut infection, gave greatly reduced germination. Treating of severely threshed kernels was found to seriously impair the germination of such seeds. Many weakened seedlings resulting from acid-dehulled kernels were predisposed to attack by certain blue mould fungi. The greater opportunity of infection afforded the pathogene, resulted in great distortion of the seedlings, accompanied by failure to reach the soil surface.

8. No genetic hypothesis can be advanced for the inheritance of reaction to U. hordei. The Glabron parent showed relatively high resistance to the form of the pathogene used, while Trebi appeared to be moderately susceptible. Considerable variability existed in the infection percentage-

of the Trebi parent. The resistance exhibited by the parents was reflected in the progeny, no transgressive segregation for greater susceptibility occurring.

9. No infection with U. nuda resulted when a method of seed inoculation was used.

10. A method of wet floral inoculation was used to induce infection with H. gramineum. Only the heads of the F_2 plants were inoculated, thus giving ratios for the F_3. The Trebi parent proved to be resistant, and the Glabron parent moderately resistant to the form of the pathogene used. The wide range of infection percentages exhibited by the Glabron parent indicated certain limiations in the inoculation methods employed. The progeny showed little evidence of transgressive segregation for greater susceptibility. Keeping parental types in mind, it is difficult to postulate any definite mode of inheritance of resistance to H. gramineum in the hybrids tested.

11. A high correlation was found to exist between height of plant and number of days to heading. A segregation for physiological factors would probably explain this association. Moderate degrees of association were found to exist between covered smut reaction and both number of days to heading and height of plant. Slight correlations existed between the different combinations of height of plant, barbing of awn and stripe disease reaction. No significant

of the Trebi parent. The resistance exhibited by the parents was reflected in the progeny, no transgressive segregation for greater susceptibility occurring.

9. No infection with U. nuda resulted when a method of seed inoculation was used.

10. A method of wet floral inoculation was used to induce infection with H. gramineum. Only the heads of the F_2 plants were inoculated, thus giving ratios for the F_2. The Trebi parent proved to be resistant, and the Glabron parent moderately resistant to the form of the pathogene used. The wide range of infection percentages exhibited by the Glabron parent indicated certain limitations in the inoculation methods employed. The progeny showed little evidence of transgressive segregation for greater susceptibility. Keeping parental types in mind, it is difficult to postulate any definite mode of inheritance of resistance to H. gramineum in the hybrids tested.

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correlations were found between stripe infection and number of days to heading; barbing of awn and covered smut reaction and between barbing of awn and mean height (one cross only).

12. A large number of smooth awned disease resistant lines of desirable agronomic types have been selected for further study. Also, seven homozygous smooth awned lines have been bulked for yield tests.

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REFERENCES.

1. BRIGGS, F.N. Dehulling barley seed with sulphuric acid to induce infection with covered smut. Jour. Agric. Res. 35 (10): 907-914. 1927.

2. BROWN, A.J. On the existence of a semi-permeable membrane enclosing the seeds of some of the Gramineae. Ann. Bot. 21: 79-87. 1907.

3. CHADDOCK, R.F. Principles and Methods of Statistics. Houghton Mifflin Co., Boston and New York, 471 pp. 1925.

4. CHRISTENSEN, J.J. and GRAHAM,T.W. Physiologic specialization in Helminthosporium gramineum. Phytopath. 22(1): 6. 1932 (Abst.).

5. CONNERS, I.L. Report on the prevalence of plant diseases in the Dominion of Canada. 1929 and 1931.

6. CONNERS, I.L., and EARDLEY, E.H. Report on the prevalence of plant diseases in the Dominion of Canada. 1930.

7. DAVID, P.A. A study of crosses between Trebi and three smooth-awned varieties of barley. Iowa State College Jour. Sci. 5(4): 285-314. 1931.

8. FARIS, J.A. Physiologic specialization of Ustilago hordei. Phytopath. 14: 537-557. 1924.

9. FARIS, J.A. Factors influencing infection of Hordeum sativum by Ustilago hordei. Amer. Jour.Bot.11: 189-214. 1924.

10. FUCHS, W. A new method for the artificial inoculation of barley with Helminthosporium gramineum, Rbh., and its application to the investigation of disinfection and immunity problems. (German) Phytopath. Zeitschr. 2 (3): 235-256. 1930. (Abst. Rev. Appl. Myc. 9(11): 710. 1930).

11. GENAU, A. Methods of artificial infection of barley with Helminthosporium gramineum and studies on the susceptibility of various summer barleys to thus fungus. (German) Kühn - Arch., 19: 303. 1928. (Abst. in Rev. Appl. Myc. 8(4): 231-232. 1929).

12. GRIFFEE, F. Correlated inheritance of botanical characters in barley and manner of reaction to Helminthosporium sativum. Jour. Agr. Res. 30(10): 915-935. 1925.

13. HARLAN, H.V. Smooth-awned barleys. Jour. Am. Soc. Agron. 12(6,7): 205-208. 1920.

14. HARLAN, H.V. and POPE, M.N. Many noded, dwarf barley. Jour. Heredity 13: 269-273. 1923.

15. HARLAN, H.V., MARTINI, M.L. and POPE, M.N. Tests of barley varieties in America. U.S.D.A. Dept.Bul.1334. 1925.

16. HARLAN, H.V. and MARTINI, M.L. Earliness in F_1 barley hybrids. Jour. Heredity, 13: 269-273. 1929.

17. HAYES,H.K.,STAKMAN, E.C.,GRIFFEE,F. and CHRISTENSEN,J.J. Reaction of barley varieties to Helminthosporium sativum. I. Varietal resistance, II. Inheritance studies in a cross between Lion and Manchuria. Minn. Agr. Exp. Sta. Tech. Bul. 21. 1923.

18. HAYES, H.K. Breeding smooth awned barleys. Jour. Hered. 17(10): 371-381. 1926.

19. HAYES, H.K. and GARBER, R.J. Breeding Crop Plants. McGraw-Hill Book Co., New York, 2nd Ed., 438 pp. 1927.

20. HOR, K.S. Interrelations of genetic factors in barley. Genetics 9(2): 151-180. 1924.

21. IMMER, F.R. Formulae and tables for calculating linkage intensities. Genetics 15(1): 81-98. 1930.

22. ISENBECK, K. Investigations on Helminthosporium gramineum Rabh., bearing on breeding for immunity.(German). Phytopath. Zeitschs. 2: 503-555. 1930. (Rev. in Pl.Br.Abst. 1(3): 367. 1931).

23. JOHNSON, T. Studies on the pathogenicity and physiology of Helminthosporium gramineum Rab. Phytopath. 15(12): 797-804. 1925.

24. MCCURRY, J.B. Report on the prevalence of plant diseases in the Dominion of Canada for the years 1927-28.

25. MIYAKE, K. and IMAI, Y. The genetic studies in barley. I. (with English resume). Bot. Mag., Tokyo, 36: 27. 1922.

26. MIYAZAWA, B. Dwarf forms in barley. Jour. Genetics,11: 205-208. 1921.

27. NEATBY, K.W. An analysis of the inheritance of quantitative characters and linkage in barley. Sci. Agr. 9: 701-718. 1929.

28. RAVN, F.K., Nogle Helminthosporium - arter og de af dem fremkaldte sygdomme hos byg og havre.Copenhagen. 1900.

13. HARLAN, H.V. Smooth-awned barleys. Jour. Am. Soc. Agro
12(6,7): 205-208. 1920.

14. HARLAN, H.V. and POPE, M.N. [illegible] naked, dwarf barley.
[illegible] 1922.

15. HARLAN, H.V., MARTINI, M.L. and POPE, M.N. Tests of
barley varieties in America. [illegible]
1925.

16. HARLAN, H.V. and MARTINI, M.L. Earliness in F_1 barley
[illegible]

17. HAYES [illegible]
Reaction of barley varieties to Helminthosporium
sativum. I. Varietal resistance. II. Inheritance
studies in a cross between Lion and Manchuria.
[illegible]

18. HAYES, H.K. Breeding smooth awned barleys. Jour. Hered
17(10): 371-381. 1926.

19. HAYES, [illegible]
McGraw-Hill Book Co., New York, 2nd Ed., 438 pp. 19

20. HOR, K.S. Interrelations of genetic factors in barley.
Genetics 9(2): 151-180. 1924.

21. [illegible]

22. ISENBECK, K. Investigations on Helminthosporium gramineum
Rabh., bearing on breeding for immunity. (German).
Phytopath. Zeitschr. 2: 503-555. 1930. (Rev. in
Pl.Br.Abst. 1(3): 367. 1931).

23. JOHNSON, T. Studies on the pathogenicity and physiology
of Helminthosporium gramineum Rab. Phytopath. 15(
797-804. 1925.

24. McCURRY, J.B. Report on the prevalence of plant disease
in the Dominion of Canada for the years 1927-28.

25. MIYAKE, K. and IMAI, Y. The genetic studies in barley.
I. (with English resume). Bot. Mag., Tokyo, 36:
[illegible]

26. MIYAZAWA, [illegible] Dwarf forms in barley. Jour. Genetics,11:
[illegible]-8. 1921.

27. NEATBY, K.W. An analysis of the inheritance of quantita
tive characters and linkage in barley. Sci. Agr. [illegible]
701-718. 1929.

28. [illegible] - [illegible]

29. ROBERTSON, D.W. Linkage studies in barley. Genetics 14: 1-136. 1929.

30. ROBERTSON, D.W., DEMING, G.W. and KOONCE, D. Inheritance in barley. J.A.R. 44(5): 445-466. 1932.

31. SIGFUSSON, S.J. Correlated inheritance of glume color, barbing of awns and length of rachilla hairs in barley. Sci. Agr. 9(10): 662-674. 1929.

32. SMITH, N.J.G. The parasitism of Helminthosporium gramineum Rab., (Abs.) Proc.Cambridge Phil. Soc. (Biol. Sci.) 1: 132-133. 1924. (Abs. in Rev. Appl. Myc. 3: 515. 1924.

33. SMITH, N.J.G. Observations of the Helminthosporium diseases of cereals in Britain. I. The behavior of Helminthosporium gramineum in a common barley disease. Ann. Appl. Biol.16(2): 236-260. 1929.

34. TAPKE, V.F. An undescribed loose smut of barley (Abst.). Phytopath. 22(10): 869. 1932.

35. TAYLOR, J.W. and ZEHNER, M.G. Effect of depth of seeding on the occurrence of loose and covered smuts in winter barley. Jour. Amer. Soc. Agron. 23: 132-141. 1931.

36. TISDALE, W.H. An effective method of inoculating barley with covered smut. Phytopath. 13: 551-554. 1923.

37. TISDALE, W.H. and TAPKE, V.F. Infection of barley by Ustilago nuda through seed inoculation.Jour. Agr.Res. 29(6): 263-284. 1924.

38. VANDERWALLE, R. Contribution à l'étude des maladies charbonneuses de l'Orge. Bulletin de L'Inst. Agron. et les Stat. de Recherches de Gembloux. 1(4): 291-322. 1932.

39. VAVILOV, N. De l'origine d'orge a barbes lesses. Bul. Appl. Bot and Pl. Breed. (1921): 12: 53-128. 1922.

40. VESTERGAARD, H.A.B. Jagttagelser vedsprande Arveleghedsforhold hos Lupin, Heveda og Byg. Tidsskr. f. Plantaol., 26: 491-510. 1919. (Orginal not seen. Rev. in Expt. Sta. Rec. 42: 133-135. 1920).

41. VOGT, E. Ein Beitrag sur Kenntnis von H. gramineum Rab., Arb Biol Reichsanst sür Land. und Forst. wirtsch.11: 387-393. 1923. (Abs. in Rev. Appl. Myc. 3: 25-27. 1924.

42. WEXELSEN, H. Linkage of a quantitative and a qualitative character in barley. Hereditas 17(3): 323-341. 1933.

43. Harlan, H.V., Pope, M.N. and Aicher, L.C. Trebi barley, a superior variety for irrigated land. U.S.D.A. Dept Circ. 208. 1922

B29741